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THE IMPORTANCE OF FOREST COVER FOR THE SURVIVAL OF OVERWINTERING MONARCH BUTTERFLIES (*DANAUS PLEXIPPUS*, DANAIDAE)

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ABSTRACT. When knocked to the ground or forced to land short of their roosts, monarch butterflies, too cold to fly, gain elevation by crawling up nearby vegetation. Although many occasionally fail to gain their roosts when returning from daily activities, they seldom remain overnight in forest clearings. Their behavior is explained by night ground temperatures being colder than those above the ground and by night temperatures under the forest canopy being warmer than those in forest clearings. If forced to remain on the ground in open areas for as little as one night, the majority suffer flight impairment or death. The meteorological conditions causing these climatic differences and the possible agent of impairment and death are discussed.

Millions of monarch butterflies spend the winter months in Mexico clustered on branches and trunks of trees. On warm days many thousands fly out of the colonies, principally to water. Depending on climatic conditions, varying numbers of healthy butterflies are found on the ground or on low foliage beneath the clusters. A few of those found on the ground are dead and yet show no obvious causes of death (Calvert et al., 1979).

Several environmental conditions can prevent butterflies from returning to roosting clusters. Falling temperatures, due to increasing cloud cover or onset of evening, effectively trap butterflies returning from daily activities when they land on the ground or low foliage. Direct physical actions of hail, rain, snow and wind also knock butterflies out of their roosts and occasionally cause butterfly-laden branches and tops of small trees to fall to the ground. After a storm butterflies continue to fall from water drenched roosts for several days (Calvert & Brower, ms. in prep.).

Once on the ground or low foliage, healthy butterflies, too cold to fly, shiver in an attempt to raise their thoracic muscles' temperature (Douglas, 1979; Kammer, 1971) to a point where they can fly back to a cluster or, if the temperature is too low for flight, attempt to crawl up any available foliage (Fig. 1). Some of these, however, due either to lack of appropriate foliage or to decreasing temperatures, are unable to get off the ground. These butterflies eventually close their wings and become dormant. Long periods of inclement weather may keep butterflies grounded for several days, because ambient thermal conditions do not reach the temperature required for flight.

These observations suggested that being forced to remain on the ground overnight or longer was potentially harmful to the butterflies and prompted experiments using naturally occurring temperature and humidity regimes. We asked, first, if inclement conditions could result in butterfly mortality and, second, what advantages roosting in the forest might provide. By comparing climatic effects of forested and open areas on butterfly mortality, we also began to inquire into the effects of local forest management on these butterflies.

MATERIALS AND METHODS

During January 1980 at a Mexican overwintering site of approximately 0.21 hectares located 2 km southeast of a previous colony designated Site Alpha (Brower et al., 1977), we exposed groups of butterflies to ambient conditions for several nights in two areas differing greatly in microclimate. In the evening when temperatures were approximately 10°C, too cold for butterflies to fly, we placed 90 butterflies obtained from a roost in the colony in three topless hardware-cloth enclosures (Fig. 2) as follows: fifteen butterflies of each sex were placed in each of two enclosures located in a 0.5- hectare deforested area (hereafter called "open area"); fifteen butterflies of each sex were also placed in an enclosure located within the colony approximately 100 m from the open area. All butterflies were in the same apparent physical condition. To keep the butterflies at ground level, we removed vertical vegetation from the enclosures and when necessary picked them off the walls.

The following day we allowed individual butterflies an opportunity to fly by tossing them into the air during a warm period when other butterflies were flying. If a butterfly flew irregularly or could not fly at all, we assigned it to one of two categories of disability: "flight impaired" or "moribund" (Table 1). Butterflies failing the initial flight test were given another opportunity to fly.

A second group of 90 butterflies was exposed for two nights before flight-testing. In addition, this group was weighed in subgroups of 15 by sex each evening and morning in order to monitor weight gained because of dew or frost (Table 2). They were also weighed each evening after all dew had evaporated to determine weight loss due to desiccation (Table 2). Those butterflies remaining after the flight-test in both groups of 90 were exposed for two additional nights, their weights recorded evening and morning, and then flight tested once again.

During the day, all butterfly groups were kept in wide mesh nylon cages shielded from direct sunlight. A Pesola 50-g balance accurate to 0.1 g was used to weigh the butterfly groups and a PSG max-min thermometer was used to monitor nightly minimum temperatures.

FIG. 1. Monarch butterflies knocked down from their roosts by a snowstorm. Some have managed to get into relatively warmer air by crawling up the stem of *Senecio angulifolius* DC. Original 35-mm Kodachrome by Willow Zuchowski.

FIG. 2. Hardware cloth enclosure used to delimit observation areas. Heavily frosted butterflies lie on the ground. Butterfly at top center (arrow) is more upright in posture and consequently did not suffer as much frosting. Inset: Enlargement of frosted butterflies in enclosure (2×). Original 35-mm Kodachrome by William Calvert.

RESULTS

Grounded butterflies exposed one or two nights in the open area experienced lower temperatures (3-night average = −1.7°C; range = −1.1 to −2.2°C) than the corresponding group within the colony (3-night average = +1.9°C; range = 2.8 to 1.1°C; Table 1). Furthermore, the open area groups took on more dew and/or frost, gaining an average of 0.15 g or 22.5% of their weight in water, compared to only 0.003 g or 0.6% for the colony groups (Table 2). The groups in the open suffered an average of 60% more flight impairment and mortality than the control groups exposed within the colony (Table 1). Expected differences due to the time exposed are also evident. After one night in the open area 40% of the butterflies flew off normally, while only 30% did so after two nights (Table 1). In addition to the data given in Table 1, at the end of two additional nights of exposure all but one of the remaining butterflies were dead or moribund. In contrast, all butterflies exposed within the colony flew off normally, even after two nights of exposure (Table 1).

Weight loss due to desiccation was small, averaging only 0.001 g or 1.5% of their body weight (Table 2). Most of this loss occurred between the third and fourth evenings, suggesting that some of the ani-

TABLE 1. The effect of exposure of grounded butterflies to nighttime conditions on flight and survivorship.

Position of enclosure	Expt.[1] no.	No. nights exposed	Percentage of butterflies at end of exposure: Normal	Flight[2] impaired	Moribund[3]	Dead	Minimum nightly ground temperature T°C
Experimentals:	1	1	47%	27%	23%	3%	−2.2
(On ground in open area adjacent to colony)	2	2	33%	47%	20%	0%	−1.7 −1.1
	3	1	33%	27%	37%	3%	−2.2
	4	2	27%	10%	60%	3%	−1.7 −1.1
Controls:	5	1	100%	0%	0%	0%	1.1
(On ground under trees within colony)	6	2	100%	0%	0%	0%	2.8 1.7

[1] Each experiment consisted of 15 ♀♀ and 15 ♂♂.
[2] Butterfly attempted to fly but landed within 10 m for 2 consecutive trials.
[3] Butterfly was alive but unable to fly.

mals may have died before the final weighings. Both the small magnitude of weight lost and the lack of difference between weight loss occurring in the colony and in the open area make weight loss an unlikely factor in the mortality of these butterflies. Since there was no net weight gain from evening to evening, it is clear that the water deposited as dew remained on the surface and was not absorbed by the animals.

DISCUSSION

This study shows that butterflies experience flight impairment and increased mortality when grounded in an open area. Normally, how-

TABLE 2. Weight gains due to nightly accumulations of dew or frost and weight loss due to desiccation. Figures are the percentage of final weights which is water.*

Position of enclosure	Expt. no.	Number of butterfly days†	Percent weight gained from evening to morning	Percent weight lost from evening to evening
Experimentals:	2	101	22.1%	2.6%
(On ground in open area adjacent to colony)	4	98	22.8%	0.9%
Controls:				
(On ground under trees within colony)	6	51	0.6%	1.1%

$* = \frac{\Sigma \text{ weight gain or loss}}{\Sigma \text{ final weights}} \times 100.$

† = Σ Number butterflies exposed each night × number of nights.

ever, butterflies do not remain overnight in cleared areas. Two factors increase the likelihood of their exposure to conditions similar to or approaching those found in open areas. (1) Periods of cold inclement weather in Mexico's transvolcanic belt lasting up to six days have been witnessed by us and are evident in local weather records kept by the Mexican National Weather Service. (2) Local logging activities, even though they do not involve clear cutting, continue to produce open spots and thinned areas, thereby reducing the moderating effect of the natural forest on extremes of temperature and humidity.

Long term weather records (10–29 years) available from eight standard meteorological stations near the overwintering areas above 2500 m altitude show monthly extreme minimum temperatures for December, January and February averaging −5.2°C, −6.4°C and −6.4°C respectively (Anon., 1976). These stations are always located in open areas where minimum temperatures would be lower than those occurring in adjacent forested areas. If damping effects of the forest are on the order of those indicated in Table 1 ($\bar{x}$ = 3.5°C), temperatures as low as −2.5°C are expected near the ground within the colonies—a temperature sufficiently low to cause flight impairment, moribundity and death after only one night of exposure (Table 1). It should be noted that the average altitude of the butterfly colonies is ca. 3000 m, while the average for the eight nearby weather stations is only 2589 m. Even colder temperatures are therefore expected at the higher overwintering colony altitudes.

Within the overwintering areas, we have personally witnessed the destructive effects of local storms during the past four years. Of particular severity were storms lasting from 6–8 February 1978 and from 21–26 January 1980. The former dropped 7-mm diameter hail pellets on at least two colonies; the latter storm brought as much as 25 cm of snow to adjacent open areas. Tens of thousands of butterflies were knocked down from their clusters, pelted with hail, and frosted or covered with snow (Figs. 3 and 4).

Since butterflies stranded on the ground in open areas experience a very different microclimate from those on the ground in the colonies, a review of some important microclimatological parameters pertinent to these altitudes is in order (see Geiger, 1965 for a more complete discussion of microclimate). The differences are primarily due to a difference in location where nighttime cooling occurs. In both open and forested areas, cooling takes place at night from all plant and soil surfaces, but, for reasons discussed below, cooling is most effective at the interface between plant and open sky, i.e., near the ground in open areas and at canopy level in forested areas. Beneath and within plant canopies, radiational cooling of any object is in general diminished by a dynamic interchange of radiation

FIGS. 3 & 4. Butterflies knocked to ground by a snowstorm. Some are partially buried in the snow (arrows). Some have oriented upslope so they can bask whenever the sun appears. Others have crawled onto low-lying vegetation. Original 35-mm Kodachrome photos by William Calvert.

involving absorption and subsequent reradiation, mainly by adjacent plant parts, but also by other adjacent objects, water vapor and CO_2 (band radiation) and the reabsorption of radiation by the object. Above the vegetational layer, however, water vapor and CO_2 play only a minor role as an impediment to outgoing radiation. Not only is the absolute humidity low during the overwintering period (this period closely corresponds to the Mexican dry season), but also at night; at these altitudes all objects are near 0°C, a temperature for which the water vapor and CO_2 absorption coefficients are very low (Geiger, 1965). Little absorption and subsequent reradiation (back radiation) takes place at the top-most plant layer since no plant parts or other objects lie above it, and water vapor and CO_2 are inefficient absorbers at temperatures prevailing at night. Heat received and stored during the day by this layer is radiated almost unhindered at night.

The primary source of heat at night is that stored in the ground. Ground heat is transferred to nearby objects by longwave radiation and eddy diffusion. In addition, the butterflies receive some heat through band radiation of atmospheric water vapor and CO_2, but this is diminished for reasons discussed above. These objects lose heat by longwave radiation to the atmosphere and cosmic cold, and by convection and evaporation. Principally, because no heat is returned by conduction as occurs in the ground, these objects cool more rapidly than the ground itself. Consequently, dew deposition and frost are likely to occur on them first (Geiger, 1965).

Thus, a butterfly grounded in an open area loses heat to the atmosphere and cosmic cold by radiational and evaporative cooling, gains none back by conduction and only a little back by absorption and reabsorption of longwave radiation or by eddy diffusion of ground heat upward. Once night sets in, a butterfly cools more rapidly than the surrounding air, dew deposition begins, and then frost occurs. On the other hand, a butterfly positioned beneath the forest canopy is in near radiational equilibrium with plant parts and other butterflies. Most of the cooling action is occurring above it at the interface of canopy and sky. Water vapor pressure within the colony is generally higher, and convection less; consequently, evaporation is less and more longwave radiation is reabsorbed. These conditions greatly moderate the low temperatures occurring in nearby open areas.

Because of these microclimatic factors, crawling up onto vegetation (Fig. 1) is an appropriate response for butterflies stranded near the ground when air temperatures preclude flight. During windless nights, movement one meter upward would take them into air that is an average of 3.3°C warmer than air at ground level (Siegel *In* Geiger, 1950). Our measurements of minimum temperatures during a clear night at Site Alpha indicated that the minimum temperature at 1-meter elevation was 2.5°C warmer than on the ground. Additional benefits of crawling onto vegetation may accrue due to increases in back radiation from overhead plant foliage and perhaps also to increased safety from small mammal predation. These aspects of this remarkable behavior are currently being investigated.

Temperature differences *per se* may not wholly account for differences in survival rates between exposed butterflies in open and forested areas. Using laboratory facilities, Urquhart (1960) subjected groups of monarchs to 12-hour low temperature regimes and found complete recovery in adults subjected to temperatures as low as −6.8°C. Since temperatures this low were never encountered by us at the Mexican overwintering sites, the incapacitation of 60% of butterflies exposed one night to a minimum temperature of −2.2°C (Table 1) suggests that frost may be more important than low temperatures *per se*.

In studies investigating the effect of moisture or ice in contact with the insect exoskeleton, Salt (1936) found that freezing moisture on the surface of an insect was effective in the initiation of freezing within by the growth or propagation of external ice into the body of the insect, a process he called inoculative freezing. No such enhancement of freezing was found, however, when ice was placed in contact with the dry surface of a cooled insect (Aoki & Shinozaki, 1953). Bevan & Carter (1980) also found moisture to be critical to mortality. Their results suggested, as do ours, that freezing of dew condensed on the insect's surface initiates internal freezing at temperatures higher than it would occur if the surface was dry. By crawling upward these butterflies escape both the higher humidities and lower temperatures found near the ground; and hence, they escape the dangers of having ice in contact with their exoskeletons.

Summary and Conclusion

Butterflies are often trapped on the ground for one or more nights, due to a variety of environmental circumstances. Ground conditions are in general colder and wetter than those prevailing above the ground. Sixty percent of butterflies exposed to ground conditions for one night in an open area suffered flight incapacitation or died. By crawling up off the ground to avoid the coldest and wettest areas, the butterflies remove themselves from the dangers of inoculative freezing.

In all but the most inclement weather, the moderating effect of the forest canopy protects the butterflies from temperature extremes; all butterflies exposed to these conditions, even though prevented from crawling off the ground, survived. However, several times a year during storms or cold spells, ground temperatures beneath the forest canopy become cold enough to incapacitate or kill them. Under these circumstances crawling up into warmer temperature zones would probably enhance their survival.

When the forest is thinned, meteorological conditions are expected to approach those found in forest clearings; the moderating effect of the forest will be diminished; butterfly mortality is expected to rise. Because of the increasing pressures of forestry in these areas of Mexico, even though the practices lie within the bounds of good forest managment, it is urgent and essential to establish relationships between weather, forest thinning, and butterfly survival in the overwintering areas.

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